Caspian Tern Predation on Salmon and Steelhead Smolts in the Columbia River Estuary

September 26, 2002

NOAA Fisheries
Portland, Oregon

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Caspian Tern with fish - Columbia Bird Research Team

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TABLE OF CONTENTS

List of Tables and Figures

EXECUTIVE SUMMARY

- Human activities have contributed to salmon and steelhead population declines in the Columbia River Basin.
- Relatively new human constructed islands in the Columbia River estuary have provided breeding habitat for Caspian terns, where they have been able to successfully exploit juvenile salmonids as a food resource.
- The effect of Caspian tern predation varies between years and among salmonid species and is greatest on steelhead and smallest on wild yearling chinook.
- Caspian tern predation on juvenile salmonids reduces salmon population growth rate and thus recovery, however, removing all tern predation will not, by itself, lead to full recovery of any listed salmon and steelhead stock.
- The effect of Caspian tern predation on recovery may be comparable to fish passage improvements at Columbia River dams and harvest reductions for some Evolutionarily Significant Units.
- Relocating Caspian terns to habitat closer to the mouth of the Columbia river significantly reduces predation impact on juvenile salmon
- Additional PIT tag data needs to be collected and evaluated to validate initial predation rates at East Sand Island.

BACKGROUND

The ecosystems inhabited by anadromous salmonids is extensive and complex. In the case of upper Columbia River and Snake River salmon and steelhead, their range extends inland as far as 1500 km and rise to elevations of 2500 m above mean sea level. Their oceanic range extends through the North Pacific Ocean to the Bering Sea and the Sea of Japan. Climate conditions and human activities have had adverse affects on water flows, river conditions, spawning and rearing habitat, ocean productivity, and eventually, salmonid survival and productivity. Wild and naturally reproducing stocks of steelhead have declined dramatically in the interior Columbia River Basin (Lee et al. 1997). Wild and naturally reproducing spring- and summer-run chinook stocks also have declined dramatically throughout the Pacific Northwest. As a result, nearly every population of naturally producing anadromous salmonids in the Columbia River Basin is now listed (or is a candidate for listing) under the Endangered Species Act (ESA).

Salmon experience high mortality rates as juveniles in freshwater, the estuary and early ocean, leading researchers to suggest that reducing mortality during the juvenile stage has the potential to increase population growth rates (Kareiva et al. 2000). Although significant mortality of juvenile salmon and steelhead occur in the ocean, our ability to influence ocean survival is limited. Therefore, improvements in freshwater survival and production are imperative and can directly affect the number of returning adult salmon and steelhead (Raymond 1988, Beamesderfer et al. 1996).

Many of the measures taken to restore anadromous salmonid production in the Columbia River Basin have focused on improving the survival of juvenile migrants through the mainstem dams. Various life-cycle models indicate that mortality of juveniles during migration in freshwater constrains anadromous salmonid production in the Columbia River Basin, thereby reducing the benefits of enhancement measures upstream (Beamesderfer et al. 1996, Kareiva 2000).

Increasing populations of piscivorous birds (primarily Caspian terns) nesting on islands in the Columbia River estuary annually consume large numbers of migrating juvenile salmonids (Roby et al. 1998) and thus constitute one of the factors that currently limit salmonid stock recovery (Roby et al. 1998; Independent Multidisciplinary Science Team 1998; Johnson et al. 1999). Therefore, reducing Caspian tern predation in the estuary, is one potential mechanism to reduce mortality, thereby increasing population growth rates of Endangered Species Act (ESA) listed salmonid Evolutionarily Significant Units (ESUs)[1] in the Columbia River Basin.

Anthropogenic changes in the Columbia River Basin appear to have facilitated increases in populations of colonial waterbirds (Roby et al. 1998). The largest recorded colony of Caspian terns in the world (Roby et al. 1998) now occupies an island created by dredging and maintaining a navigation channel in the Columbia River estuary. There, the terns feed on large numbers of migrating juvenile salmon and steelhead (Table 1). Basinwide losses to avian predators now constitute a substantial proportion of individual salmonid runs (Roby et al. 1998).

In the early 1990s, National Marine Fisheries Service (NOAA Fisheries) staff at the Point Adams Field Station noted substantial increases in the size of newly established Caspian tern nesting colonies on man-made islands in the Columbia River estuary (Figure 1). Several estuary islands on which piscivorous birds nest (Figure 2) were created from, or augmented by, materials dredged to maintain the Columbia River Federal Navigation Channel. There were no recorded observations of terns nesting in the Columbia River estuary before 1984 when about 1000 pairs apparently moved from Willapa Bay to nest on newly deposited dredge material on East Sand Island. Those birds moved to Rice Island in 1986. The number of Caspian terns nesting in the estuary has since expanded to 9,000-10,000 pairs, the largest colony ever reported. In 1999, the colony was encouraged to relocate to East Sand Island. In 2001, the majority of the West Coast population

[1] Under the Endangered Species Act, the National Marine Fisheries Service (NOAA Fisheries) lists species, subspecies and distinct population segments of vertebrates. NOAA Fisheries policy stipulates that a salmon population will be considered distinct if it represents an "evolutionary significant unit" (ESU) of the biological species (Waples 1991). For the purposes of conservation under the ESA, an Evolutionarily Significant Unit (ESU) is a distinct population segment that is substantially reproductively isolated from other conspecific population units and represents an important component in the evolutionary legacy of the species (Waples 1991).

nested on just four acres on East Sand Island and in 2002 on six acres on East Sand Island.

Because of the growing concern over the increasing impacts of avian predation on salmonid smolts, NOAA Fisheries required the Bonneville Power Administration (BPA) and U.S. Army Corps of Engineers (COE) to conduct an analysis of avian predation in the Columbia River estuary and, if necessary, to develop potential measures for managing the predator populations. These requirements were part of the 1995 Formal Consultation on the Operation of the Federal Columbia River Power System and Juvenile Transport Program (NMFS 1995). Oregon State University (OSU) and the Columbia River Inter-Tribal Fish Commission (CRITFC) began conducting the research in 1996. The concern over large losses of salmonid smolts to newly established and rapidly expanding numbers of avian predators stems from the fact that currently 12 ESUs of anadromous salmonids native to the Columbia River Basin are listed as threatened or endangered under the ESA (Figures 3 and 4).

Because avian predation on salmonids is a multi-jurisdictional issue, NOAA Fisheries, COE, U.S. Fish and Wildlife Service, BPA, CRITFC, and the resource agencies of the states of Washington, Idaho and Oregon formed the Caspian Tern Working Group (CTWG) to develop a long-term management plan for reducing tern predation in the estuary. As part of this effort, the CTWG is evaluating the benefit of dispersing Caspian terns to good habitat away from the main salmonid migration corridor of listed Columbia River ESUs without affecting overall tern survival. In addition, NOAA Fisheries is evaluating the overall risk tern predation presents to listed salmonid populations.

The intent of this document is to summarize what is known about Caspian tern predation impacts to salmonids in the Columbia River estuary. Information gained from recovery of PIT tags and a bioenergetic model providing estimates of predation rates on juvenile salmon are described. How the information is applied in a life-cycle model to determine the extent of the impacts and the benefits of relocating terns to other habitats are also described. This information may be utilized by resource managers to develop management options to reduce predation impacts.

CASPIAN TERNS (*Sterna caspia*)

Caspian terns are highly migratory and are nearly cosmopolitan in distribution (Harrison 1983; Harrison 1984). Nesting has been reported from Baja California to the Bering Sea, from the Gulf Coast of Texas to Lake Athabasca, and from the Florida panhandle to Labrador - as well as in Australia, New Zealand, South Africa, Asia, and Europe.

The West Coast population winters in Southern and Baja California and returns north to nest (Harrison 1983; Harrison 1984). Early colony size estimates in the Pacific Northwest showed as many as 500 pairs mixed with gulls and cormorants as far north as Klamath Lakes in Oregon (Harrison 1984). Some nesting colonies were first discovered in Washington near Moses Lake and Pasco in the 1930s, but coastal nesting was not recorded until the late 1950s, when a colony nested in Grays Harbor (Alcorn 1958, Penland 1976, 1981). Since the early 1960s, the population has shifted from small colonies nesting in interior California and Southern Oregon to large colonies nesting on human-created habitats along the coast (Gill and Mewaldt 1983). The current population in the Columbia River Basin is part of a dramatic north- and coastward expansion in the range and an overall increase in Caspian tern numbers in western North America.

The numbers of Caspian terns in western North America more than doubled between 1980 and 1999 (Cuthbert and Wires 1999). A reason for this increase is that human-created habitat provides high quality nest sites and is associated with population increases in many parts of North America (Cuthbert and Wires 1999). In the Columbia River estuary, numbers of Caspian terns have increased from a few scattered individuals before 1984 to nearly 20,000 in 2000 (Figure 1).

Caspian terns arrive in the Columbia River estuary in April and begin nesting at the end of the month (Roby et al. 1998). To avoid predators, terns construct their nests on islands (Harrison 1984) and show a preference for barren sand. They are piscivorous in nature (Harrison 1984), requiring about 220 grams (roughly one-third of their body weight) of fish per day during the nesting season. The timing of courtship, nesting and chick rearing corresponds with the outmigration of many of the salmonid stocks in the basin (Collis et al. 2002) (Figure 5).

PREDATION IMPACTS

Two approaches have been taken to evaluate the extent of salmonid mortality resulting from Caspian tern predation. Since 1997, biologists with the BPA funded research project ("Avian Predation on Juvenile Salmonids in the Lower Columbia River," - a joint project of OSU, U.S. Geological Survey, CRITFC, and Real Time Research Consultants) have observed salmonid consumption at tern colony sites and utilized a bioenergetics model[2] to provide estimates of mortality. The second approach is analyses of the number of passive integrated transponders (PIT) tags detected on the tern colonies to estimate salmonid predation rates by ESU (Collis et al. 2001b, Ryan et al. 2001).

These analytical approaches indicate that salmon and steelhead constituted a major portion of tern diets when the birds nested on Rice Island. For example, diet analysis in 1997 and 1998 indicated that 77.1% and 72.7%, respectively, of prey items consumed by Caspian terns nesting on Rice Island were juvenile salmonids (Collis et al. 2002). During the peak of smolt out-migration through the estuary for yearling chinook salmon, coho

[2]A description of the bioenergetics model used to develop the estimate may be found in Roby et al. (1998).

salmon and steelhead, which coincides with the tern incubation period in May, the diet of Caspian terns was consistently over 90% juvenile salmonids (Collis et al. 2002).

This concentration on smolts as a food source translates into substantial juvenile mortality during the outmigration period. Roby et al. (In Review) used a bioenergetics model to estimate that in 1998, Caspian terns nesting on Rice Island consumed about 11.2 million juvenile salmonids. Best estimates of smolts consumed since 1997 are listed in Table 1.

Table 1. Estimates of juvenile salmonids (in millions) consumed by Caspian terns in the Columbia River estuary 1997-2001[3] and numbers reaching the estuary[4] .

Year	Number of Smolts Consumed (95% confidence interval in parentheses)	Estimated number of smolts migrating to the estuary
1997	7.48 (5.36 - 9.6)	57.5
1998	11.2 (8.3 - 14.2)	116.9
1999	11.7 (9.4 - 14.0)	86.3
2000	7.3 (6.1 - 8.6)	117.3
2001	5.9 (4.8 - 7.0)	96.4

In 1997 and 1998, between one and two million salmonid smolts listed under the ESA entered the Columbia River estuary. This represented about one or two percent of the total of all salmonid smolts estimated to be migrating to the estuary. However, in 1999, seven more ESUs of anadromous salmonids in the Columbia River Basin were listed, and roughly 6 million listed smolts entered the estuary along with over 80 million unlisted smolts (primarily of hatchery origin). The majority of juvenile salmonids in the estuary are of hatchery origin and the majority being consumed by Caspian terns are hatchery fish (Independent Multidisciplinary Science Team 1998). Overall, Caspian terns consumed approximately 6% to 14% of the estimated outmigrating population of juvenile salmonids originating from the Columbia River basin.

Since 1987, researchers in the Columbia River Basin have placed over five million PIT tags in juvenile salmonids for various studies (Ryan et al. 2001). Identifying PIT tags on

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[3] Collis et al. 2001a.

[4] Data from NOAA Fisheries Fish Ecology Division and Fish Passage Center. No estimates were made for steelhead in 1997. Includes estimated numbers of hatchery coho salmon only, no estimates are available for wild coho. Since no values for coho survival through the power system are available, estimates of survival of hatchery coho through the system were developed through the use of SIMPAS (NMFS 2000a) values for yearling chinook.

Rice and East Sand Islands can provide a minimum estimate of proportion of the stocks that were consumed by terns in these colonies. In recent years, approximately one million juvenile salmonids have been PIT tagged annually (Collis et al. 2001b)[5]. Using tag detection equipment, over 115,000 PIT tags were detected on Rice Island in 1998 and 1999 (Ryan et al. 2001). Collis et al. (2001b) indicate that the majority of these PIT tags detected were from chinook, coho and sockeye salmon, and steelhead. Of the PIT tags placed in steelhead smolts in 1997 that were detected at Bonneville dam, 2.8% of wild smolts and 5.4% of hatchery-raised smolts were subsequently detected on the Rice Island tern colony (Collis et al. 2001b). For those steelhead PIT-tagged in 1998 and detected at Bonneville Dam, 11.7% of wild smolts and 13.4% of hatchery-raised smolts were subsequently detected on the Rice Island tern colony (Collis et al. 2001b). For yearling chinook salmon PIT-tagged in 1998 and detected at Bonneville Dam, 0.5% of wild smolts and 1.6% of hatchery-raised smolts were subsequently detected on the Rice Island tern colony (Collis et al. 2001b).

Ryan et al. (2002 in review), analyzing PIT tag data from 1998 to 2000 on Rice Island and East Sand Island, determined that steelhead experienced higher predation rates (0.6% to 8.1% on East Sand Island and 1.3% to 9.4% on Rice Island) than chinook salmon (0.2% to 2.0% on East Sand Island and 0.6% to 1.6% on Rice Island). Additional PIT tag data from East Sand Island in 2001 and 2002 has yet to be analyzed. This data should provide a better evaluation of any changes in predation rates that may have been realized by relocating the colony to East Sand Island.

There are some important uncertainties and findings derived from estimating predation rates of salmon by Caspian terns. First, predation impacts derived from PIT tags (although a more direct measure of predation than that derived from a bioenergetic model) represent a minimum estimate of proportion of the stocks that were consumed because an unknown number of tags are regurgitated or defecated off the colony site, wind and water erosion removes an unknown number, some tags may have been damaged and not detectable by the equipment, and not all tags are detected (Ryan et al. 2001, Collis et al. 2001b, Collis et al. 2002). Secondly, predation rates vary annually and by the methodology used to make the estimate, making it difficult to derive a single predation rate. Although there is good correspondence of predation rates between methodological estimates, utilizing the upper and lower bounds of the predation rates to bracket potential recovery improvements represent the most reliable approach that currently should be used to assess potential impacts of smolt predation by Caspian terns. Finally, it is clear that predation rates are not uniform for all salmon species, thus evaluation of the impact of Caspian tern predation should be salmon species specific, to the extent possible.

[5] The vast majority of PIT- tagged juvenile salmonids are from Snake River ESUs, primarily steelhead and chinook.

NOAA Fisheries has developed a life cycle model - under the auspices of the Cumulative Risk Initiative at the Northwest Fisheries Science Center - to assess salmonid population trends and the impact of an anthropogenic activity on those trends (Appendix 1). This model has application when mortality rates can be constructed and attributed to a particular activity. The value of life cycle models derive from providing an objective outcome for comparing the influence of various factors influencing population growth rates, rather than attempting to estimate real gains from any management action. Assessing the impact of predation by Caspian terns on juvenile salmonids during a particular life history phase is amenable to such an evaluation.

Using the CRI model, we have estimated the impact of Caspian tern predation on the population growth rate (lambda) for predation estimates ranging from 1% to 20% for each species. Estimates of Caspian tern predation rates have ranged from approximately less than 0.5%, for wild yearling chinook salmon to approximately 14% for steelhead (Ryan et al. In review, Roby et al. In press). To provide examples of potential gains from any management action, we have provided percent change of ESU specific population growth rates assuming complete or 50% removal of terns (Tables 2 and 3, respectively). In addition, we have translated the information into a family of curves that bracket the range of predation rates to estimate the impact of predation on population growth rates by species (Figure 6) if complete removal of terns was achieved. As an example, using Equation [3] (Appendix 1), and a hypothetical predation rate of 5% for Snake River steelhead, a maximum potential improvement in population growth rate of 1.077% would be realized if this mortality could be completely eliminated (Table 2 and Figure 6). If the predation rate was reduced by 50%, the impact on that ESU specific population growth rate would improve approximately .530% (Table 3). Clearly, the magnitude of potential improvement to the population growth rate is dependent upon the degree to which mortality can be reduced (Tables 2 and 3 and Figure 6).

For comparative purposes, changes called for in NOAA Fisheries' FY 2000 Biological Opinion on operation of the hydropower system (FCRPS), to improve passage for both adults and juveniles are anticipated to increase population growth rates by approximately 1-2 % for the Snake River Spring/Summer-run chinook salmon ESU and nearly 5% for the Snake River Fall-run chinook salmon ESU (NMFS 2000b). Harvest on the Snake River summer/chinook ESU consists only of a minimal tribal ceremonial and subsistence harvest; eliminating it altogether would improve population growth rate by 1-2% (McClure et al., in review). The Upper Columbia River Spring-run chinook salmon ESU has similarly low harvest rates, but several other ESUs have sustained higher harvest rates and consequently benefit more from harvest reduction.

Several factors must be kept in mind when interpreting the results of these calculations, however. Perhaps the most important factor is that this type of calculation assumes that there is no compensatory mortality later in the life cycle, and that any reduction in tern predation is fully realized. Given these limitations and uncertainties, the estimates of percent change in population growth rates should be viewed as maximum potential improvements. The realized improvements in population growth would likely be lower from any management action reducing tern predation impacts on salmon ESU's. In addition, from a management perspective, these results may not be as easy to achieve as they are to calculate. For instance, the relationship between tern abundance and predation rate is not well known, which makes it difficult to directly relate and substantiate with data how a change in colony size may affect predation rates.

RELOCATION EFFORTS

In 1999, 2000, 2001 and 2002, efforts to relocate the terns to East Sand Island were undertaken. These efforts have apparently been successful in reducing consumption of smolts without affecting tern productivity.[6] Caspian tern diets of almost exclusively salmonids at Rice Island (77% and 90% in 1999 and 2000) shifted to 46%, 47% and 33% salmonids at East Sand Island in 1999, 2000 and 2001 respectively (Collis et al. 2001a, Roby et al. in press). This represents substantial declines in juvenile salmonid mortalities. Confirmation of these findings was substantiated by observations identifying a significant reduction in the number of PIT tags detected per pair of terns on East Sand Island compared to tern pairs on Rice Island in 1999 and 2000 (Table 4) (Ryan et al. 2002 in review). In 2000, smolt consumption was estimated at 7.3 million, a 4.4 million reduction compared to 1999 - the last time terns nested on Rice Island (Collis et al. 2001a, FWS 2001). Consumption of salmonid smolts in 2001 was estimated at 5.9 million - a 5.9 million reduction compared to 1999 (Collis et al. 2001a). In addition, Caspian tern productivity at East Sand Island in 2001 was the highest recorded for terns nesting in the estuary (Collis et al. 2001a). It is apparent that relocating terns to an alternate nesting island reduced consumption of juvenile salmon without adversely affecting tern population growth rates.

Table 4. Ratio of PIT tags detected per pair of nesting Caspian terns in 1999 and 2000

	1999	2000
Rice Island	0.6	1.2
East Sand Island	0.3	0.3

CONCLUSION

[6] The CTWG relocated the Caspian tern colony from Rice Island to East Sand Island in an attempt to decrease salmonid losses by moving the tern colony to a site with abundant alternate prey sources. Over the last two years, with abundant alternate prey species, consumption of salmonids was less than previous years. Relocating the colony to the lower island, which is closer to periodically abundant engraulids and clupeids, has contributed to the reduction. Moreover, nesting success has also been substantially higher for Caspian terns nesting on East Sand Island as compared to Rice Island (Roby et al. in press).

Not all listed salmonid populations have declined because of the same factors or combination of factors, and not all populations could be expected to respond positively to any particular management measure or combination of measures. In the case of the avian predator populations discussed here, artificial islands (such as Rice Island) have promoted the development of unprecedentedly large colonies of piscivorous birds with subsequent increases in losses of juvenile salmonids from predation.

Evaluations of salmonid predation by Caspian terns indicate that substantial numbers of juvenile salmonids are being consumed. Two approaches to evaluate the extent of that impact yield similar results, verifying and providing reasonable estimates of predation rates. PIT-tag recoveries on Rice and East Sand Island reveal species specific vulnerability to Caspian tern predation, demonstrating that steelhead are substantially more susceptible to tern predation than yearling chinook. Efforts to reduce predation by moving the colony from Rice Island (more central to the Columbia River estuary) to East Sand Island (located towards the mouth of the Columbia River) have successfully decreased overall predation as fewer salmon are consumed per pair of terns on East Sand Island. The decrease in consumption has been substantial. However, PIT tag data on predation rates needs to be further collected at East Sand to confirm initial observations and to document that the relocation efforts have been successful in reducing impacts for all ESUs (particularly for steelhead).

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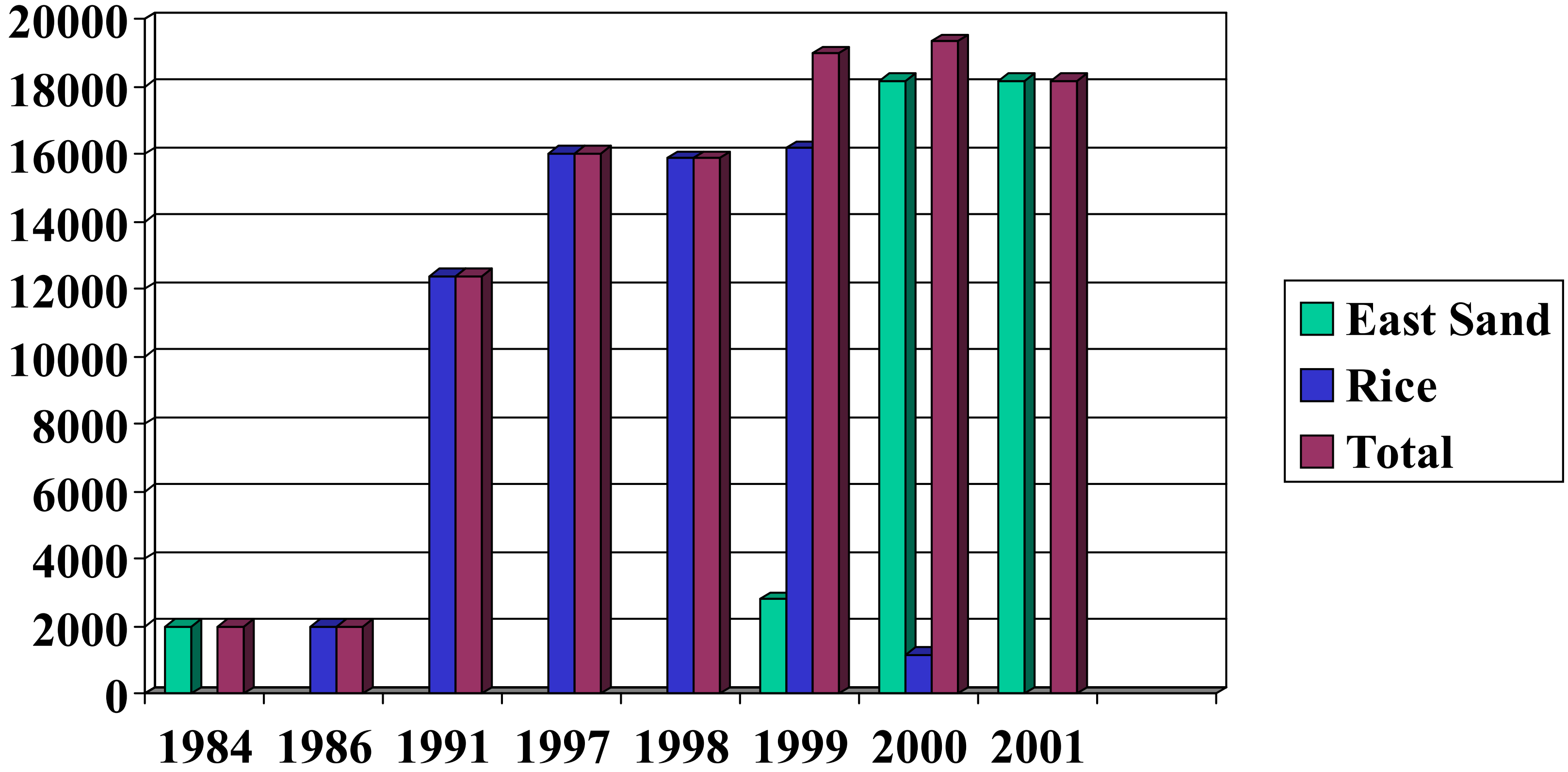

Figure 1. Numbers of Caspian terns utilizing islands in the Columbia River estuary for nesting since 1984.

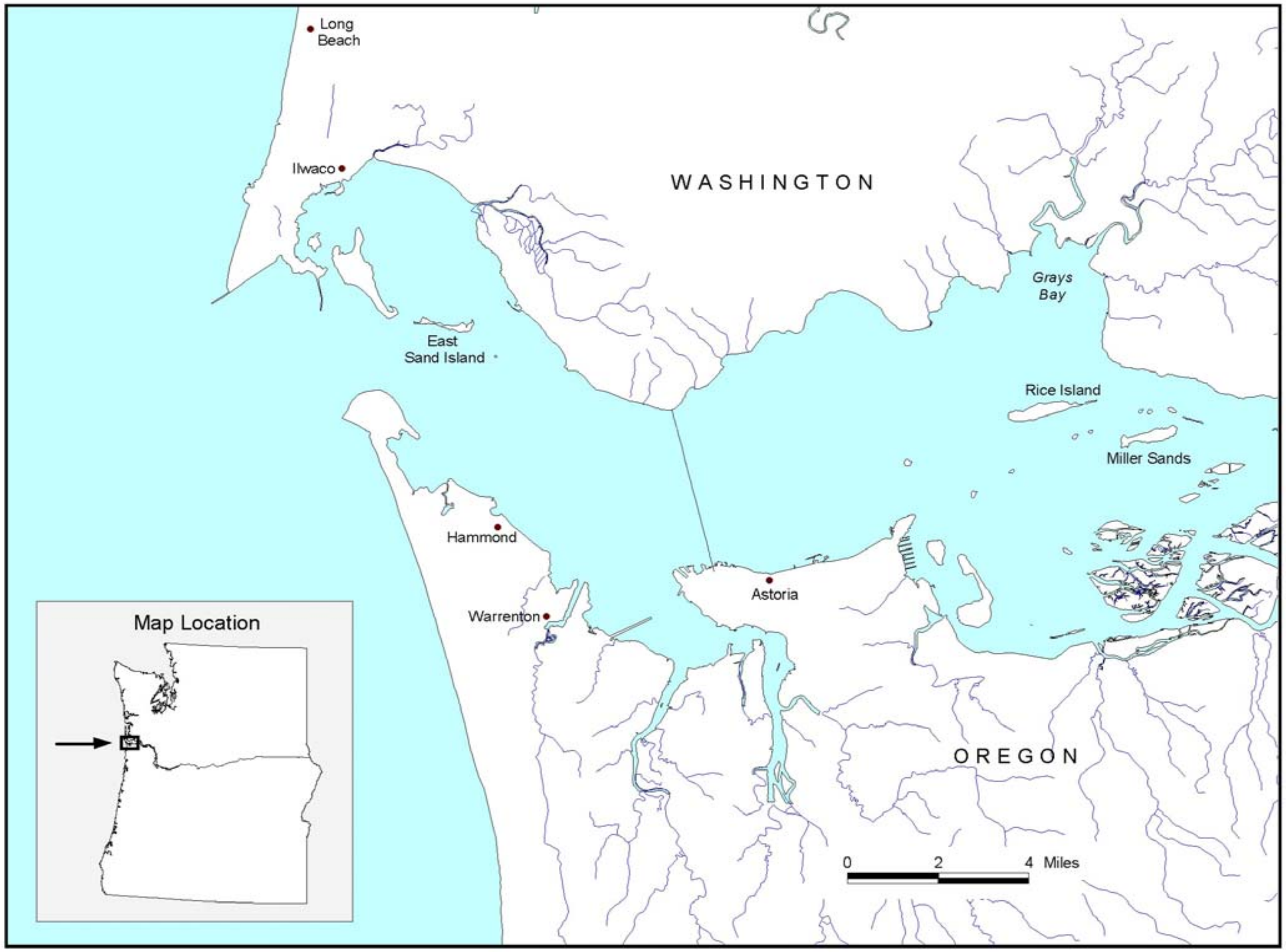

Figure 2. Map of the Columbia River estuary showing the relative locations of East Sand and Rice Islands, sites of Caspian tern nesting colonies.

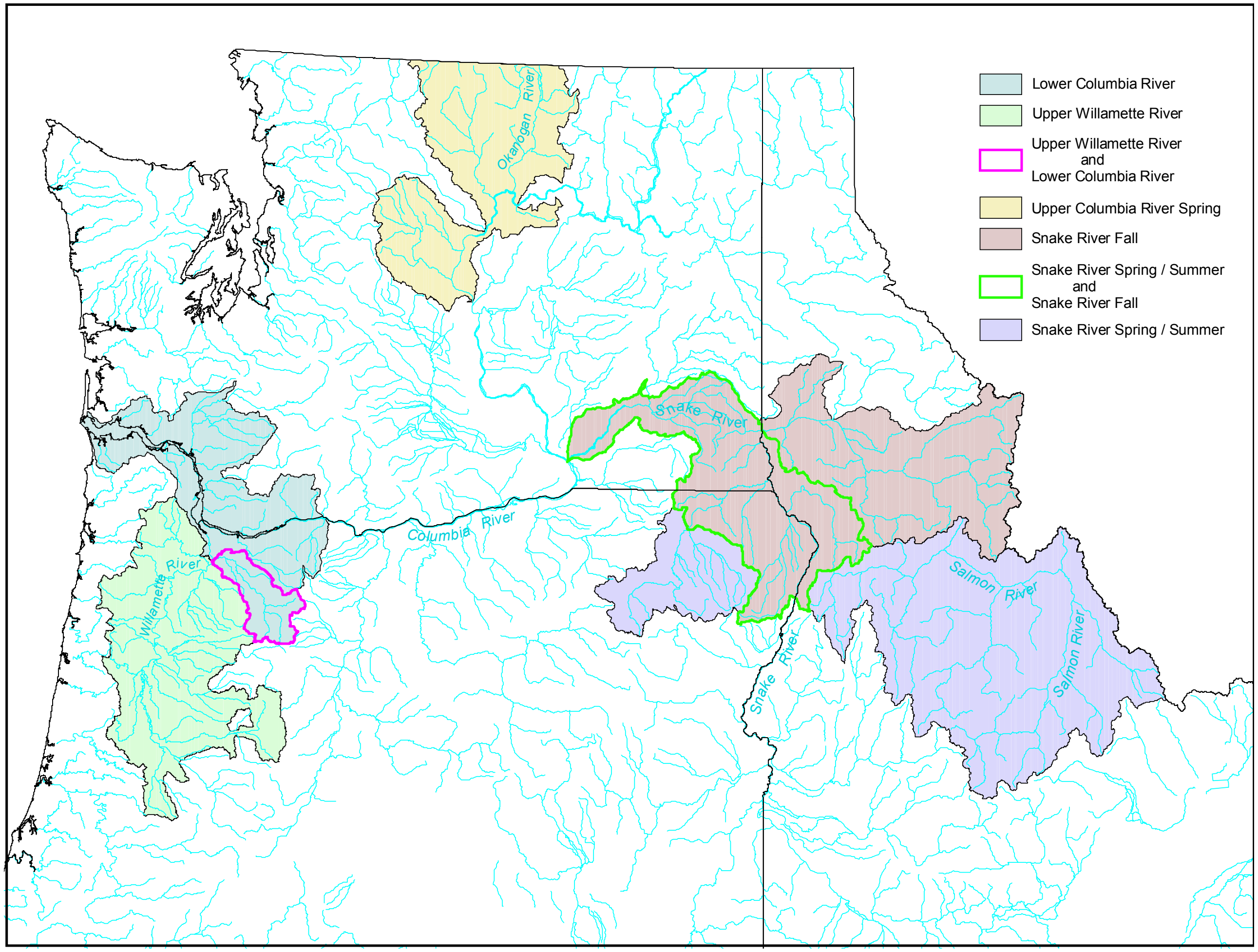

Figure 3. Map of Columbia River Basin listed chinook salmon ESUs.

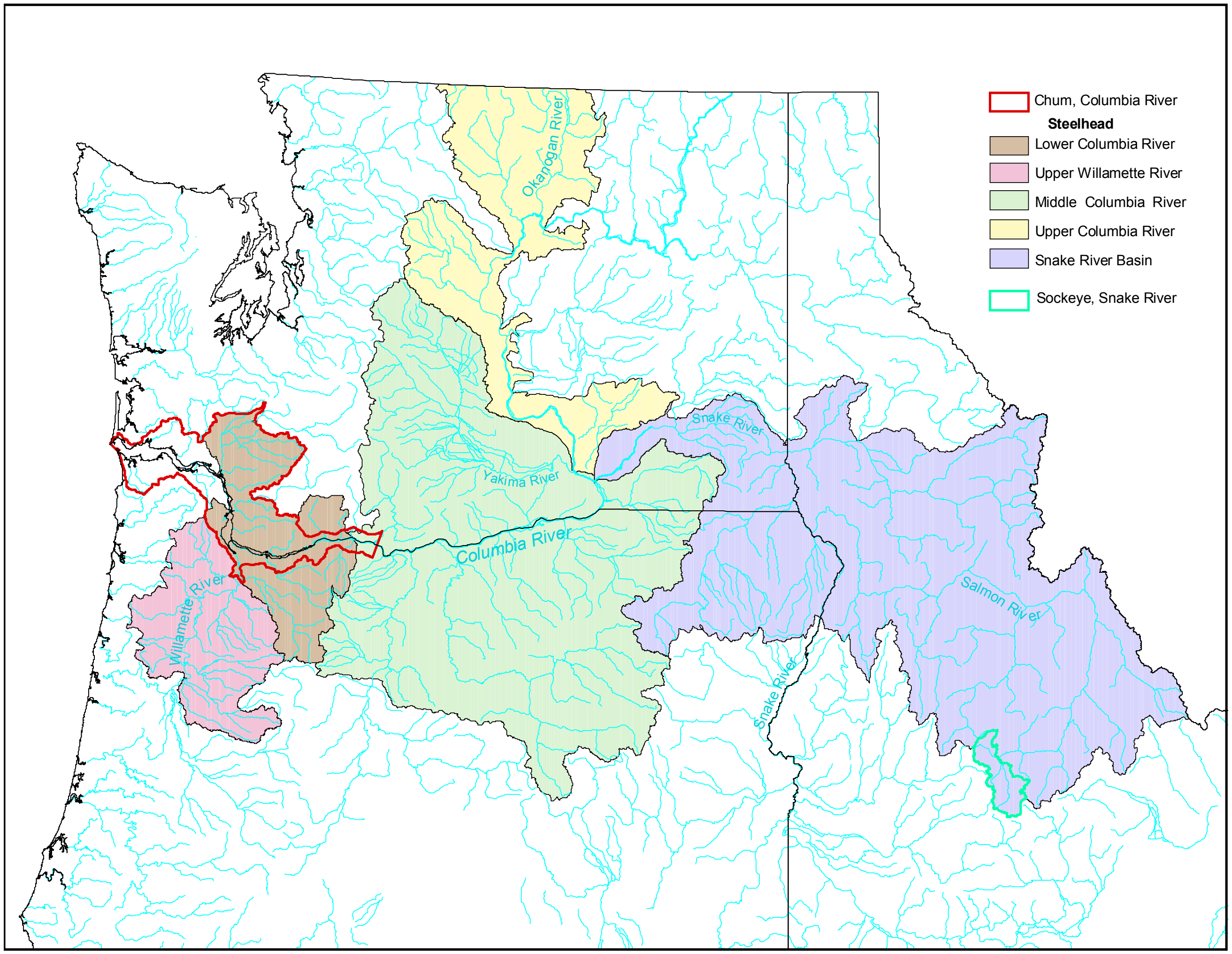

Figure 4. Map of the Columbia River Basin listed steelhead, sockeye and chum salmon ESUs.

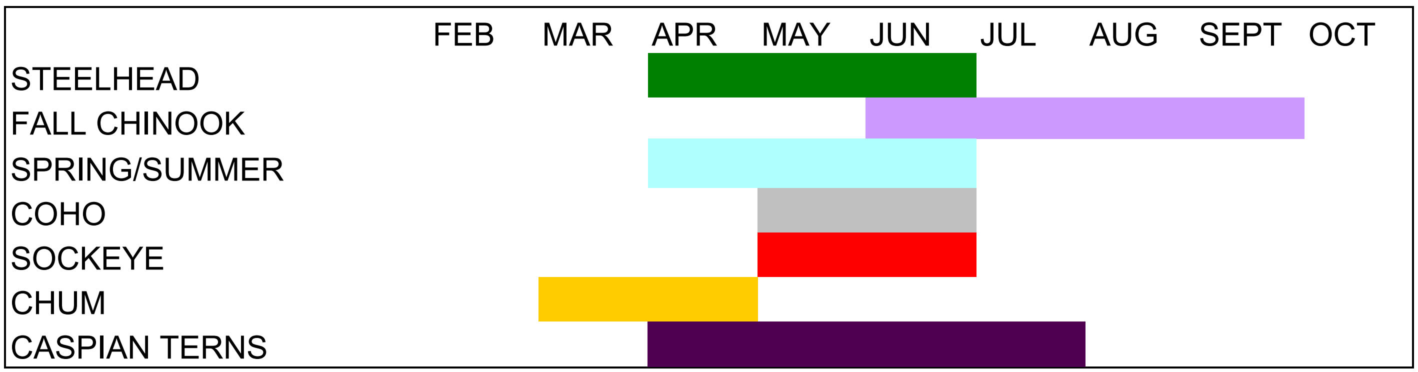

Figure 5. Arrival times of juvenile salmonids and nesting period of Caspian terns in the Columbia River estuary.

Table 2. Estimated percent change in population growth rate assuming complete elimination of tern predation of varying rates for listed salmonid ESUs in the Columbia River Basin. Predation rate represents the total fraction of listed juvenile salmon consumed by terns.

Predation Rate	Snake River spring/summer chinook	Snake River Fall Chinook	Snake River Steelhead	Upper Columbia Chinook	Upper Columbia Steelhead	Mid-Columbia Steelhead	Upper Willamette Chinook	Upper Willamette Steelhead	Lower Columbia Chinook	Lower Columbia Steelhead	Columbia River Chum
1.0%	0.234	0.274	0.210	0.236	0.267	0.207	0.227	0.247	0.298	0.217	0.279
2.5%	0.591	0.692	0.530	0.595	0.675	0.523	0.573	0.622	0.752	0.548	0.704
5.0%	1.201	1.407	1.077	1.208	1.372	1.063	1.165	1.265	1.529	1.114	1.431
6.1%	1.476	1.730	1.323	1.485	1.686	1.306	1.431	1.555	1.880	1.369	1.759
9.3%	2.298	2.695	2.059	2.312	2.627	2.033	2.228	2.421	2.930	2.131	2.741
10.0%	2.482	2.912	2.224	2.498	2.839	2.196	2.407	2.616	3.166	2.302	2.962
20.0%	5.330	6.269	4.769	5.365	6.108	4.708	5.166	5.622	6.825	4.938	6.376
Generation Time	4.297	3.67	4.79	4.27	3.764	4.85	4.43	4.08	3.38	4.63	3.61

Table 3. Estimated percent change in population growth rate assuming a 50% reduction in tern predation, given current predation of varying rates for listed salmonid ESUs in the Columbia River Basin. Predation rate represents the total fraction of listed juvenile salmon consumed by terns.

Predation Rate	Snake River spring/summer chinook	Snake River Fall Chinook	Snake River Steelhead	Upper Columbia Chinook	Upper Columbia Steelhead	Mid-Columbia Steelhead	Upper Willamette Chinook	Upper Willamette Steelhead	Lower Columbia Chinook	Lower Columbia Steelhead	Columbia River Chum
1.0%	0.117	0.137	0.105	0.117	0.133	0.103	0.113	0.123	0.148	0.108	0.139
2.5%	0.293	0.343	0.263	0.295	0.335	0.260	0.284	0.309	0.373	0.272	0.349
5.0%	0.591	0.692	0.530	0.595	0.675	0.523	0.573	0.622	0.752	0.548	0.704
6.1%	0.723	0.848	0.649	0.728	0.826	0.641	0.702	0.762	0.921	0.671	0.862
9.3%	1.114	1.306	0.999	1.121	1.273	0.987	1.081	1.174	1.419	1.034	1.328
10.0%	1.201	1.407	1.077	1.208	1.372	1.063	1.165	1.265	1.529	1.114	1.431
20.0%	2.482	2.912	2.224	2.498	2.839	2.196	2.407	2.616	3.166	2.302	2.962
Generation Time	4.297	3.67	4.79	4.27	3.764	4.85	4.43	4.08	3.38	4.63	3.61

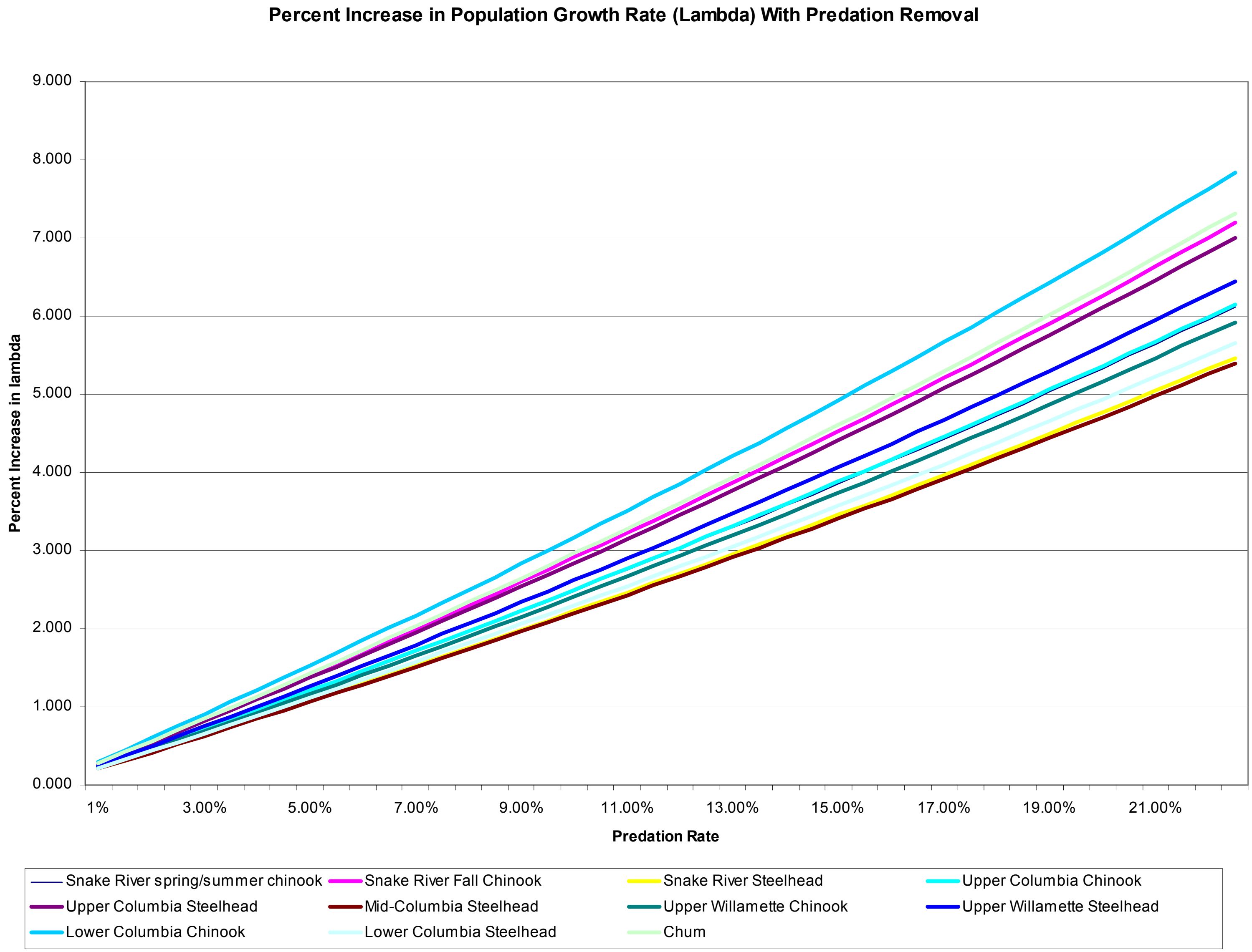

Figure 6. Percent increase in population growth rate (Lambda) with Caspian tern predation removal

APPENDIX 1

Cumulative Risk Initiative

The net reproductive rate for any population, across its entire life cycle is the combined survival rates across all life stages multiplied by the combined fecundity rates across all ages (Caswell 2000, pg. 126):

$$R_0 = F_1 + S_1{*}F_2 + S_1{*}S_2{*}F_3 + S_1{*}S_2{*}S_3{*}F_3 \ldots \qquad [1]$$

where S_1 is the survival rate of age 1 individuals, S_2 is the survival rate of age 2 individuals, etc., F_1 is the fecundity of age 1 individuals, F_2 is the fecundity of age 2 individuals, etc and n is the number of stages into which the life cycle has been divided. The net reproductive rate is also known as the recruits (to the spawning grounds) per spawner, *R/S*, for salmonids. For the salmonids discussed here, $F_1 = 0$, since reproduction dues not occur during the first year of life. The annual rate of population growth can be approximated as follows (Caswell 2000, pg. 129):

$$\lambda = R_0^{\ 1/generation\ time} = R/S^{\ 1/generation\ time} \qquad [2]$$

This equation provides a metric, λ, for comparison between species (or ESUs) with different generation times.

If a change in survival occurs before reproduction (e.g. at the smolt stage), then ($R_{0,\mathrm{new}}/R_{0,\mathrm{old}}$) would reduce to ($S_{\mathrm{new}}/S_{\mathrm{old}}$). Thus the proportional change in λ due to a change in smolt survival rate at a single stage is straightforward:

$$\begin{aligned} P=(\lambda_{\mathrm{new}}-\lambda_{\mathrm{old}})/\lambda_{\mathrm{old}} &= R_{0,\mathrm{new}}^{\ 1/generation\ time} / R_{0,\mathrm{old}}^{\ 1/\mathrm{generation\ time}} - 1 \\ &= (R_{0,\mathrm{new}}/R_{0,\mathrm{old}})^{1/generation\ time} - 1 \\ &= (S_{\mathrm{new}}/S_{\mathrm{old}})^{1/generation\ time} - 1 \end{aligned} \qquad [3]$$

where P is the proportional change, S_{new} is the new (changed) survival rate, and S_{old} is the original survival rate.